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INFRAGENERIC TAXONOMY OF NEW WORLD *ERIGERON* (COMPOSITAE: ASTEREAE)

Guy L. Nesom
Department of Botany, University of Texas, Austin, Texas 78713 USA

ABSTRACT

In a synopsis of infrageneric taxonomy of New World *Erigeron*, *E. uniflorus* L. is accepted as the lectotype of sect. *Erigeron*; other lectotypes are proposed for a number of sections or generic segregates by G. Don, Nuttall, de Candolle, Rafinesque, Torrey & Gray, Botschantzev and Vierhapper. Eighteen sections, counting sect. *Leptostelma* of South America, are currently recognized in the New World, eight of which are new: sect. **Arenarioides**, sect. **Imbarba**, sect. **Cincinnactis**, sect. **Karvinskia**, sect. **Osteocaulis**, sect. **Scopulincola**, sect. **Spathifolium** and sect. **Spinosi**. Five of these are segregates from sect. *Erigeron* sensu Cronquist. Sect. **Linearifolii**, comb. nov., replaces sect. *Pycnophyllum* Cronq. The justification for maintaining *Darwiniothamnus* as a distinct genus is weak; it should be returned to *Erigeron*. **Erigeron veracruzensis** nom. nov. replaces the later homonym *E. scaberrimus* (Less.) Nesom.

KEY WORDS: *Erigeron*, Asteraceae, New World, systematics.

I present a synopsis of the taxonomy and nomenclature of the New World (primarily North American) species groups of *Erigeron*. In this, I have attempted to list all of the accepted species that occur in North America (including México) and Central America. I have not dealt with South American species included by Solbrig (1962) in sect. *Erigeron*; I am studying the species of *Erigeron* (ca 20) in the Antilles. This infrageneric taxonomy certainly will undergo modifications as concepts of relationships within the genus are developed and refined and as other names may be discovered in surveys of older literature. I believe it is important, however, to point out as clearly as possible the great amount of diversity that exists within *Erigeron*. This is particularly significant as botanists begin comprehensive investigations of the relationships among genera of Astereae. The approach taken here differs strongly from Cronquist's more inclusive view (1947) of sect. *Erigeron*, which I have partitioned into eight sections. Such hypotheses represent a step toward understanding phylogenetic patterns within this large group of species, and I believe there is at least heuristic value in presenting them as formal taxonomic proposals.

The "probable relationships" diagram presented by Cronquist (1947, p. 125) and the comments in the text of his revision have been valuable in indicating groups of inter-related species, and his insights remain largely correct. In attempting simply to delimit monophyletic groups, however, I hope to provide a useful and more objective taxonomy. Even then, because of the large degree of suspected morphological parallelism in the genus, hypotheses regarding the constitution of single lineages are speculative to a degree, but those regarding the phyletic derivations between species and lineages are even more so. Molecular approaches may be more incisive than strictly morphological ones in discovering patterns of common ancestry.

In my opinion, among the most important morphological characters for indicating sectional relationships in *Erigeron* are the behavior of the ligules of the ray flowers (coiling, reflexing, remaining straight, or closing upwards at night) and the behavior of the buds (erect, sharply nodding or arching-pendant). These are features of necessity observed in the field, because they often are not preserved in pressed and dried specimens. The plant habit and the nature of leaf insertion are also significant. Clasping leaves are almost completely restricted to the plants of sect. *Cincinnactis*, sect. *Fruticosus*, sect. *Olygotrichium* and sect. *Polyactis*, although this feature is not strictly diagnostic of any of these groups. Leaf lobing or toothing is characteristic of only six sections. Some species of sect. *Wyomingia* typically have numerous (4-14) achenial ribs in contrast to the usual number in the genus, two per achene. I believe that achene shape will also prove to be a significant feature in assessing relationships, but I have not emphasized that feature in this study. Basally caducous pappus bristles occur in only one section (sect. *Polyactis*), where they are diagnostic.

Asa Gray recognized six sections of *Erigeron* in 1841 but by 1884 had reduced the number to three (sects. *Erigeron, Trimorpha* and *Caenotus*), submerging the others into sect. *Erigeron*. Cronquist included 99 of the 133 of the North American species (in 1947) in a heterogeneous sect. *Erigeron*. Solbrig (1960, 1962), too, placed most of the South American species of the genus in sect. *Erigeron*, recognizing only three species in sect. *Leptostelma* (see below).

In a treatment of the Compositae of the U.S.S.R, Botschantzev (1959) recognized three subgenera: subg. *Erigeron* (four sections), subg. *Trimorpha* (two sections), and subg. *Conyzastrum* (Boiss.) M. Pop. [sect. *Conyzastrum* and sect. *Psychrogeton* (Boiss.) Botsch.]. The latter section was recently treated by Grierson & Reichinger (1982) as a separate genus, and I regard *Trimorpha* as a genus distinct from *Erigeron* (Nesom 1989b). I attempted to deal with some of Botschantzev's nomenclature here because a few of the

Asian and American species and groups cross the Bering Straits and occur on both continents. *Conyzastrum* and *Psychrogeton* are not included, because all the species appear to be Asian.

Among the first sectional names in *Erigeron* were those proposed in 1830 by G. Don in Loudon's *Hortus Britannicus* (see Sundberg & Jones 1987; 1988). Most of Don's groups in *Erigeron* were highly polyphyletic, and I have tried to lectotypify them in a way that will displace as few new names as possible in *Erigeron* and related genera. The name of one of Don's sections, however, must supplant a name in current usage, and one of them in *Aster*, as recently lectotypified with a species of *Erigeron* by Sundberg & Jones, assumes a position of priority over a name already in use in *Erigeron*.

Nuttall (1818, 1840) proposed names for several sections of *Erigeron* and I have tried to maintain these with appropriate lectotypes where possible. Such is also true for names proposed by Torrey & Gray (1841).

Rydberg (1906, 1918) introduced numerous infrageneric names as subheadings of his keys to species of *Erigeron*. In an earlier paper (Nesom 1982), I did not regard these as formal taxonomic proposals because Rydberg gave no indication of the intended rank of these groups and provided neither descriptions nor diagnoses. Further, several species of *Erigeron* key out in more than one subdivision. Here, however, following Jones (1980) in *Aster*, I have adopted Holmgren's point of view (1979) in regarding Rydberg's names as validly published, unranked species groups that may be used as basionyms in future combinations. In contrast, Macbride & Payson (1917) accepted one of Rydberg's aggregate names (see sect. *Tridactylia* below) with the following rationale: "... from the fact that the name was given in the plural form and appears to be just above the rank of species it may well be considered as designating a series ... ." Thus, I have attributed this formal taxon primarily to Macbride & Payson, not as a combination, in exception to Holmgren's view.

Rydberg in 1906 clearly had a view of taxonomy in *Erigeron* that encompassed more than only the Colorado species, because the names of several species groups (e.g., *Acres, Radicati, Decumbentes*) were based on epithets of taxa occurring in the Great Plains but not in Colorado. In Rydberg's broader treatment of 1918, each of these three groups included the species upon which its name was based. I have accepted these species as the types of their nomenclaturally corresponding sections, since I believe that clearly was Rydberg's intention.

The following text presents sections of *Erigeron*, generic segregates, and groups originally in *Erigeron* but transferred into other genera. Unless specifically stated to the contrary, all infrageneric names cited are in *Erigeron*. Species marked by an asterisk (*) are ones that occur strictly in México and/or Central America. Names of accepted sections as well as lists of species are presented alphabetically. Comments on putative relationships are in the text.

I follow Cronquist (1947) and Hultén (1968) in conforming to the use of masculine endings in *Erigeron*, although Linnaeus regarded the genus as neuter. The International Code of Botanical Nomenclature (1988) notes that *Erigeron* is a masculine name "for which botanical usage has re-established the classical gender despite another choice by Linnaeus."

I. SECTIONS OF *ERIGERON*

Erigeron sect. **Arenarioides** (Rydb.) Nesom, comb. et stat. nov. Based on *Erigeron* (sp.-group) *Arenarioides* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. arenarioides* (D. Eaton ex A. Gray) Rydb.

Additional species in sect. *Arenarioides: E. salmonensis* Brunsfeld & Nesom, ined. (Brunsfeld & Nesom [in press]).

These two species clearly are closely related between themselves, and I can find no other group whose unity would not be unsettled by their inclusion. Cronquist (1947) has suggested that *Erigeron arenarioides* may be related to *E. oxyphyllus* (see comments under sect. *Oxyphyllum). Erigeron nematophyllus* shares features of habit with these two species, but it has prominently coiling ligules and I include it in sect. *Wyomingia.*

Sect. *Arenarioides* is characterized by the following: tap-rooted perennials; caudex branches with densely packed, adherent leaf bases, each branch producing erect, wiry, distally branched stems; leaves ascending-appressed, entire; buds erect; heads turbinate-campanulate; and ray flowers few, with ligules not reflexing or coiling.

Sect. *Asteroidea* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:308. 1841. LECTOTYPE (designated here): *E. decumbens* Nutt. Nuttall also included *E. corymbosus* Nutt., *E. filifolius* Nutt., *E. foliosus* Nutt., *E. nanus* Nutt., *E. ochroleucus* Nutt., *E. pedatus* Nutt. (=*E. compositus* Pursh) and *E. radicatus* Hook.

Erigeron sect. *Pseuderigeron* Torrey & A. Gray, Fl. N. Amer. 2(1):177. 1841. LECTOTYPE (designated here): *E. caespitosus* Nutt. Torrey & Gray also included *E. filifolius* Nutt., *E. douglasii* Torrey & A. Gray (=*E. foliosus* Nutt.), *E. decumbens* Nutt., *E. corymbosus* Nutt. and *E. ochroleucus* Nutt.

Erigeron sect. *Stenactis* Torrey & A. Gray, Fl. N. Amer. 2(1):172. 1841. LECTOTYPE (designated here): *E. pumilus* Nutt. Other species included by Torrey & Gray: *E. glaucus* Ker Gawler, *E. speciosus* (Lindley) DC., *E. glabellus* Nutt., *E. concinnus* (Hook. & Arn.) Torrey & A. Gray. See discussion in Nesom (in press).

Asterigeron Rydb., Fl. Rocky Mts. 891. 1918. TYPE: *A. watsonii* (A. Gray) Rydb. [= *Erigeron watsonii* (A. Gray) Cronq.].

Erigeron (sp.-group) *Caespitosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. caespitosus* Nutt.

Erigeron (sp.-group) *Decumbentes* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. decumbens* Nutt.

Erigeron (sp.-group) *Pumili* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. pumilus* Nutt.

Erigeron (sp.-group) *Radicati* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. radicatus* Hook.

Erigeron (sp.-group) *Asperuginei* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. asperugineus* (D.C. Eaton) A. Gray.

Erigeron (sp.-group) *Laetevirentes* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. laetevirens* Rydb. (=*E. ochroleucus* Nutt.).

Erigeron (sp.-group) *Filifolii* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. filifolius* (Hook.) Nutt.

The plants of sect. *Asteroidea* are perennials from thick taproots (except in the *E. ursinus* group) producing mostly scapose, monocephalous stems. Also, the leaves are entire; the buds are erect; the disc corollas are narrowly tubular; the ligules of the ray corollas often dry dark blue and have a tendency (strong in some, weak or not at all evident in others) to coil at the tips, but others appear to reflex (see comments below); and the achenes tend to be narrowly oblong. The plants typically grow in open, level or sloping, sometimes rocky sites at medium elevations, often with sagebrush. Both Torrey & Gray and Nuttall saw the reality of this section, because sect. *Pseuderigeron* and sect. *Asteroidea* as originally described each included only a single species that I believe is part of a different lineage. Cronquist's "Group X" of his sect. *Erigeron* (1947) also included mostly species of sect. *Asteroidea*.

I have divided sect. *Asteroidea* into several groups and listed the species accordingly.

1. The *E. decumbens* group : *E. asperugineus* (D. Eaton) A. Gray, *E. canaani* Welsh (=*E. eatonii* sensu Strother & Ferlatte, 1988), *E. decumbens* Nutt., *E. eatonii* A. Gray, *E. jonesii* Cronq., *E. lassenianus* E. Greene (incl. *E. flexuosus* Cronq.), *E. nevadincola* S.F. Blake, *E. sonnei* E. Greene, *E. wahwahensis* Welsh (=*E. jonesii* sensu Strother & Ferlatte, 1988) and *E. watsonii* (A. Gray) Cronq.

This group is characterized by simple caudices (multicipital caudices occur but uncommonly), strongly decumbent stem bases that are often purplish, and a thickened node of wood and old petiole bases at the root-stem junction.

The leaves of all species except *E. watsonii* typically or at least frequently have 3-nerved leaves.

Strother & Ferlatte (1988) revised the taxonomy of this group, which they referred to as "*Erigeron eatonii* and allied taxa" According to them, all of the taxa of this group "... seem to be very closely related; they variously intergrade morphologically and may constitute a single, polymorphic species." I believe two additional species belong with this species group: *Erigeron asperugineous*, which previously has been thought to be more closely related to *E. clokeyi* (Cronquist, 1947; Ake, 1984) and the diminutive *E. watsonii*, although it is apparently set apart from the rest.

2. The *E. ursinus* group : *E. gracilis* Rydb. and *E. ursinus* D. Eaton.

These two species are a very closely related pair distinct from the other species of sect. *Asteroidea* in their somewhat diffuse system of rhizomes. In their purple, decumbent stem bases, they appear to be most similar to the *E. decumbens* group.

3. The *E. caespitosus* group: *E. abajoensis* Cronq., *E. awapensis* Welsh, *E. caespitosus* Nutt., *E. maguirei* Cronq., *E. nauseosus* (M.E. Jones) A. Nels., *E. ovinus* Cronq., *E. subglaber* Cronq., *E. vetensis* Rydb. and *E. zothecinus* Welsh.

This group is characterized by multicipital caudices and relatively broad, often 3-nerved basal leaves. There is some overlap in morphology with the *E. decumbens* group. Further, the ray corollas of *E. vetensis* and *E. nauseosus* have ligules that appear to reflex, setting these two species apart from the others and perhaps linking them with the *E. pumilus* group. In placing *E. zothecinus* here, I follow Welsh (1986) who compared it to *E. abajoensis* in the diagnosis.

4. The *E. corymbosus* group: *E. corymbosus* Nutt., *E. filifolius* Nutt. and *E. ochroleucus* Nutt. (incl. *E. lackschewitzii* Nesom & Weber).

These three species have narrowly lanceolate or oblanceolate leaves and the ligules of the ray flowers are typically long and prominently coiling at the tips. *Erigeron filifolius* and *E. corymbosus* typically have branched stems; *Erigeron ochroleucus* is variable in this respect and in other features.

5. The *E. radicatus* group : *E. disparipilus* Cronq., *E. latus* (A. Nelson & Macbr.) Cronq., *E. nanus* Nutt., *E. parryi* Canby & Rose, *E. poliospermus* A. Gray, *E. pygmaeus* (A. Gray) E. Greene, *E. radicatus* Hook. and *E. rydbergii* Cronq.

The *Erigeron radicatus* group is characterized by multicipital caudices and strictly erect, relatively short, linear to narrowly oblong or narrowly oblanceolate, 1-nerved, basal leaves.

6. The *E. pumilus* group: *E. aphanactis* (A. Gray) E. Greene, *E. clokeyi* Cronq., *E. concinnus* (Hook. & Arn.) Torrey & A. Gray, *E. engelmannii* A. Nels. and *E. goodrichii* Welsh.

The species of the *Erigeron pumilus* group are similar in habit and leaf shape to the *E. radicatus* group or perhaps somewhat intermediate to those of the *E. radicatus* and *E. caespitosus* groups. The *E. pumilus* group tends to be strikingly hispid in appearance, and most significantly, the ligules of the ray corollas appear to reflex. I have not seen *E. goodrichii* but tentatively include it here on the basis of the discussion by Welsh (1983), who noted that its affinities are with *E. clokeyi* and *E. asperugineous.*

Groups 4-6 of sect. *Asteroidea* are much in need of a comprehensive taxonomic study that includes field observations. The apparent occurrence of two distinctive ligule behaviors suggests that two lineages may be involved and that the groups as I have arranged them may be somewhat artificial.

**Erigeron coronarius* E. Greene, **E. janivultus* Nesom and three undescribed species perhaps belong here, near the *E. pumilus* group. I am currently studying this group and defer making a formal judgment on its taxonomic placement until the completion of the study.

Erigeron sect. **Cincinnactis** Nesom, sect. nov. TYPE: **Erigeron longipes* DC.

> Folia marginibus dentatis, gemmae plus minusve erectae, corollae radii numerosae in 1-3 seriebus cincinnatae ad maturitatem plerumque perangustae, achenia brevi-oblongae parvulae costis manifeste aurantiacis, pappus plerumque sine serie externa.

Additional species in sect. *Cincinnactis*: **E. basilobatus* S.F. Blake, **E. crenatus* Eastw., **E. exilis* A. Gray, **E. narcissus* Nesom, **E. oaxacanus* Greenman, *E. procumbens* (Houston ex P. Miller) Nesom (=*E. myrionactis* Small), **E. socorrensis* I.M. Johnston, **E. tephropodus* Nesom, **E. veracruzensis* Nesom and **E. stanfordii* I.M. Johnston ex Nesom.

The peculiar habit of *Erigeron exilis* is similar to that of species of sect. *Linearifolii*, but the behavior of its ligules allies it with sect. *Cincinnactis.*

In an earlier publication (Nesom & Sundberg 1985), I included *Erigeron longipes* as a synonym of *Erigeron scaberrimus* (Less.) Nesom. The two, however, are distinct species. Further, the name *E. scaberrimus* had already been proposed for a South American species, making my combination a later homonym. A new name is provided here for the Mexican species, which occurs from Tamaulipas, Veracruz, Puebla and Oaxaca.

Erigeron veracruzensis Nesom, nom. nov. Based on *Aster scaberrimus* Less., Linnaea 5:143. 1830. *E. scaberrimus* (Less.) Nesom, 1985; non *E. scaberrimus* Gardner, 1848.

A group of primarily Caribbean species with tightly coiling ligules apparently also belongs in *Erigeron* sect. *Cincinnactis.* Two of them, *E. bellioides* DC. and *E. cuneifolius* DC., occur in México, where they probably are adventive.

The plants of sect. *Cincinnactis* are characterized by the following: leaves with toothed margins, buds nodding; rays usually filiform and numerous (up to 300) in 1-3 series, tightly coiling at maturity, or only at the tips in species with longer ligules, usually very narrow; achenes short-oblong and very small, with prominent orange ribs; pappus usually without an outer series. All but one species (*E. narcissus*) are perennials from short, fibrous-rooted rhizomes. All are from México and Central America although *E. procumbens* ranges northward into the southeastern United States.

Sect. *Erigeron* L., Sp. Pl. 863. 1753. LECTOTYPE (see discussion below): *E. uniflorus* L.

Linnaeus included the following species in *Erigeron*:

E. uniflorus L.

E. acris L.

E. alpinus L.

E. philadelphicus L.

E. carolinianus L. (see Fernald 1944, and comments below, following "GENUS UNKNOWN."

E. canadensis L. [=*Conyza canadensis* (L.) Cronq.]

E. bonariensis L. [=*Conyza bonariensis* (L.) Cronq.]

E. gramineus L. [=*Arctogeron gramineus* (L.) DC.]

E. siculus L. [=*Pulicaria sicula* (L.) Moris]

E. camphoratus L. [=*Pluchea camphorata* (L.) DC.]

E. tuberosus L. [=*Jasonia tuberosa* (L.) DC.]

E. viscosus L. [=*Inula viscosa* (L.) Aiton]

Erigeron sect. *Uniflori* G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: *E. uniflorus* L. Don also listed *E. alpinus* L., *E. compositus* Pursh and *E. gramineus* L. [=*Arctogeron gramineus* (L.) DC.].

Aster sect. *Pauciflori* G. Don in Loudon, Hort. Brit. 346. 1830. LECTOTYPE (Sundberg & Jones 1987): *A. pulchellus* Willd. (=*Erigeron venustus* Botsch.).

Erigeron (sp.-group) *Uniflori* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. uniflorus* L.

Erigeron sect. *Monocephali* Vierh., Beih. Bot. Centralbl. 19:492. 1906. LECTOTYPE (designated here): *E. uniflorus* L.

Erigeron sect. *Siphonoglossa* Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16:393. 1954. TYPE: *E. uniflorus* L.

Erigeron sect. *Platyglossa* Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16:388. 1954. TYPE: *Erigeron venustus* Botsch.

Sect. *Platyglossa* is tentatively included as a synonym of sect. *Erigeron* although Botschantzev included in it several species that are members of sect. *Fruticosus* [e.g., *E. peregrinus* (Banks ex Pursh) E. Greene, *E. thunbergii* A. Gray]. *Erigeron venustus* does not appear to be closely related to these species (Nesom 1982) but rather to be more similar to those of sect. *Erigeron.*

Additional North American species of sect. *Erigeron: E. algidus* Jepson (=*E. petiolaris* E. Greene, non Vierh.), *E. alpiniformis* Cronq., *E. arthurii* B. Boivin, *E. aureus* E. Greene, *E. eriocephalus* Vahl, *E. evermannii* Rydb., *E. flettii* G.N. Jones, *E. grandiflorus* Hook., *E. humilis* Graham, *E. hultenii* Spongberg, *E. hyperboreus* E. Greene, *E. lanatus* Hook., *E. melanocephalus* A. Nelson, *E. mexiae* K. Becker, *E. muirii* A. Gray, *E. simplex* E. Greene, *E. yukonensis* Rydb.

This view of sect. *Erigeron* restricts it essentially to monocephalous plants of alpine and subalpine habitats, at least in North America. In addition, these plants are perennials from short, fibrous-rooted rhizomes and have entire leaves, erect buds and coiling ligules. Spongberg (1969), who included most of these species in a biosystematic study, found evidence for reticulate interrelationships among a number of them. He observed that "in North America, few species at lower altitudes in the Cordillera appear to be truly implicated with arctic-alpine species of *Erigeron*" and that their nearest relatives are "likely to be found in the mountains of Central Asia and the Caucasus."

Species with a monocephalous habit are found in every section of *Erigeron* except sect. *Arenarioides* (two species), sect. *Oxyphyllum* (two species) and sect. *Phalacroloma* (two species, perhaps belonging with sect. *Olygotrichium*). In sects. *Fruticosus*, *Karvinskia, Leptostelma, Olygotrichium* and *Polyactis*, it seems relatively clear that branched capitulescences are primitive, but in the other groups, including sect. *Erigeron*, it seems likely that monocephaly is primitive and that a branching habit has been derived from ancestors with simple, monocephalous stems.

In searching for an area of common ancestry between *Erigeron* and *Aster*, Cronquist (1947) emphasized the branching, leafy, *Aster*-like habit of species of *Erigeron* sect. *Fruticosus.* There are boreal, monocephalous species of *Aster*, however, that also appear to straddle a different, somewhat arbitrary morphological boundary between *Aster* and *Erigeron*, e.g., *A. alpinus* L. and *A. alpigenus* (Torrey & A. Gray) A. Gray.

Two lectotypes have been selected for *Erigeron* by previous botanists.

E. acris L. [Britton N.L. & A. Brown, Illus. Fl. N. U.S. (ed. 2) 3:436. 1913].

E. uniflorus L. (Green, M.L., Prop. Brit. Bot. 181. 1929).

I accept *Erigeron uniflorus* as the lectotype and reject the earlier choice for several reasons. Most significantly, the choice of *E. acris* as the type of *Trimorpha* and later of *Erigeron* sect. *Trimorpha* were made before its selection by Britton & Brown as the lectotype of *Erigeron* (sect. *Erigeron*). Further, the relatively few (ca 40-45) species of sect. *Trimorpha* are very distinct in their trimorphic florets from the remainder of the genus. *Trimorpha* has been treated as a genus (Vierhapper 1906) and as a subgenus (Botschantzev 1959), and I have resegregated it as a genus (Nesom 1989b). In this case, if *E. acris* were the type of *Erigeron*, more than 300 species would have to be renamed in a genus now understood to be one of the various synonyms of *Erigeron*. Finally, the choice of the generic name ("early old age") by Linnaeus probably was intended to reflect the appearance of the densely woolly-villous involucres of some of the species. *Erigeron uniflorus* shows this feature, *E. acris* does not.

Cronquist (pers. comm.) has added his agreement with this choice of a lectotype with the following comment: "Pennell pointed out to me many years ago that Linnaeus often based his descriptions for Genera Plantarum on a single species, which if it can be identified becomes the logical lectotype. Linnaeus' description in Genera Plantarum is scarcely compatible with *E. acris*, although it would fit *E. uniflorus* and some other species."

Sect. *Fruticosus* G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: "*E. glaucus* B.R." (=*E. glaucus* Ker Gawler, Bot. Reg., 1815). Monotypic as recognized by Don.

Erigeron sect. *Pauciflori* G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (designated here): *E. bellidifolius* Willd. (=*E. pulchellus* Michx.). Don also included *Erigeron caucasicas* Stev., *E. nudicaulis* Michx. (=*E.vernus* (L.) Torrey & A. Gray), *E. glabellus* Nutt., *E. jamaicensis* L. and *E. montevidensis* Spreng. [according to Solbrig (1962), this plant probably represents a species of *Conyza*].

Musteron Rafin., Fl. Tellur. 2:50. 1836. TYPE: "*M. bellidifolium*" Rafin. Probably =*E. bellidifolius* Willd. (=*E. pulchellus* Michx.). Monotypic as recognized by Rafinesque.

Fragmosa Rafin., Fl. Tellur. 2:50. 1836. LECTOTYPE (designated here): *E. nudicaulis* Michx. [=*E. vernus* (L.) Torrey & Gray]. Also included in *Fragmosa* by Rafinesque were *E. uniflorus* L., *E. alpinus* L., *E. pumilus* Nutt., *E. asper* Nutt. (=*E. glabellus* Nutt.) and *E. glabellus* Nutt.

Woodvillea DC., Prodr. 5:318. 1836. TYPE: *W. calendulacea* DC. (=*E. glaucus* Ker Gawler). Monotypic as recognized by de Candolle.

Erigeron sect. *Phoenactis* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:310. 1840. LECTOTYPE (designated here): *E. speciosus* (Lindl.) DC. Other species included by Nuttall: *E. macranthus, E. hispidum* Nutt. (=*E. glaucus* Ker Gawler), *E. maritimum* Nutt. (=*E. glaucus* Ker Gawler).

Erigeron sect. *Erigeridium* Torrey & A. Gray, Fl. N. Amer. 2(1):176. 1841. TYPE: *E. vernus* (L.) Torrey & A. Gray. Monotypic as recognized by Torrey & Gray (see comments below).

Erigeron (sp.-group) *Elatiores* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. elatior* (A. Gray) E. Greene.

Erigeron (sp.-group) *Salsuginosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. salsuginosus* (Rich.) A. Gray [=*E. peregrinus* subsp. *callianthemus* (E. Greene) Cronq.]. See Cronquist (1947), however, for comments on the misapplication of the name *Aster salsuginosus* Rich.

Erigeron (sp.-group) *Macranthi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. macranthus* Nutt. [=*E. speciosus* (Lindl.) DC.].

Erigeron (sp.-group) *Glabelli* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. glabellus* Nutt.

Erigeron (sp.-group) *Asperi* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. asper* Nutt. (=*E. glabellus* Nutt.).

Erigeron (sp.-group) *Verni* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *E. vernus* (L.) Torrey & A. Gray

Erigeron (sp.-group) *Pulchelli* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *E. pulchellus* Michx.

Erigeron sect. *Peregrinus* Nesom, Syst. Bot. 7:463. 1982. TYPE: *E. peregrinus* (Banks ex Pursh) E. Greene. In an earlier paper (Nesom 1982), I included 34 species in this section but now believe that eight (those lacking a pappus of bristles) should be segregated as a distinct group (see sect. *Imbarba* below).

Species of sect. *Fruticosus*: *E. aliceae* J. Howell, *E. arizonicus* A. Gray, *E. cascadensis* A. Heller, *E. cervinus* E. Greene, *E. coulteri* Porter, *E. elatior* (A. Gray) E. Greene, *E. eximius* E. Greene, *E. formosissimus* E. Greene, *E. garrettii* A. Nelson, *E. glabellus* Nutt., *E. glaucus* Ker Gawler, *E. hessii* Nesom, *E. howellii* A. Gray, *E. kuschei* Eastw., *E. leibergii* Piper, *E. oreganus* A. Gray, *E. peregrinus* (Pursh) E. Greene, *E. platyphyllus* E. Greene, **E. potosinus* Standley, *E. pulchellus* Michx., *E. rusbyi* A. Gray, *E. rybius* Nesom, *E. sanctarum* S. Watson, *E. speciosus* (Lindley) DC., *E. subtrinervis* Rydb., *E. supplex* A. Gray, *E. thunbergii* A. Gray "complex," *E. uintahensis* Cronq. and the *E. palmeri* group (see below).

Sect. *Fruticosus* is characterized by the following: perennials mostly from short, thick, fibrous-rooted rhizomes; leaves often 3-nerved, entire or less commonly slightly toothed, the cauline more or less equably distributed, little reduced from the basal, usually at least the upper or lower clasping; buds erect or on slightly curved peduncles; phyllaries in 2-4 equal or nearly equal series, herbaceous, narrowly lanceolate with attenuate, often flexuous tips; ray corollas usually long and coiling at the tips. See Nesom (1982) for comments on problems in circumscribing this group and a discussion on a putative relationship between sect. *Erigeron* and sect. *Fruticosus*.

The *E. palmeri* group.

Four pappose species restricted to México, closely inter-related among themselves, appear to be members of sect. *Fruticosus*: **E. hintoniorum* Nesom, **E. morelensis* Greenm., **E. palmeri* A. Gray and **E. wellsii* Nesom.

Erigeron vernus (L.) Torrey & A. Gray of the southeastern United States, also belongs to the *E. palmeri* group. This species was the basis for the monotypic sect. *Erigeridium* of Torrey & Gray, but Cronquist (1947) included it as a member of sect. *Olygotrichium*. It has smaller heads on more branched stems than its closest relatives, but the thick, dull green and nearly glabrous basal leaves with remotely and shallowly toothed margins are nearly identical to those of *E. palmeri*. Further, both species have thick, fibrous roots with no rhizome. The long disc style appendages of *E. vernus*, the erect buds and the rays not closing upwards at night are also distinctive.

The position of *Erigeron pulchellus*.

The only species of sect. *Fruticosus* besides *Erigeron vernus* in the eastern United States is *E. pulchellus*. Earlier (Nesom 1982), I was equivocal about its taxonomic placement. It is similar to *E. philadelphicus* (sect. *Olygotrichium*) in aspects of its capitular morphology and its numerous, thin-herbaceous, clasping, cauline leaves. Clasping leaves, however, are also typical of sect. *Fruticosus*, and I believe Cronquist (1947) was correct in noting the distinctness of the scale-leaved, stoloniform rhizomes of *E. pulchellus*. Similar rhizomes are not produced in sect. *Olygotrichium*, but they are found in several species of sect. *Fruticosus* (e.g., *E. rybius, E. eximius, E. potosinus*). Further, *E. pulchellus* has erect buds and large heads with rays that do not close upwards at night, and the ligules of some collections can be seen to be distinctly coiling, all traits typical of sect. *Fruticosus* but found in no species of sect. *Olygotrichium*.

Erigeron sect. Imbarba Nesom, sect. nov. TYPE: **Erigeron galeottii* (A. Gray ex Hemsley) E. Greene.

> Gemmae erectae, phyllaria 2-porcata ad basim, corollae radii cincinnatae ad maturitatem, setae pappo carentes vel paucae dispersim praesentes.

Additional species in sect. *Imbarba*: **E. astranthioides* De Jong & Nesom, **E. forreri* (E. Greene) E. Greene, **E. fraternus* E. Greene, **E. guatemalensis* (S.F. Blake) Nesom, **E. mimus* (S.F. Blake) Nesom and **E. strigulosus* E. Greene.

I first included these eight species (Nesom 1982) as members of sect. *Peregrinus* (=sect. *Fruticosus*) but now believe there is as much evidence to suggest they represent a sister taxon of the latter as a derivative group of it (Nesom in prep.). These species are distinguished by their toothed leaves, erect buds, basally 2-ridged phyllaries, distally coiling ligules of the ray flowers and essential lack of pappus bristles. Except for *E. strigulosus*, a taprooted annual, they are all perennials from short, fibrous-rooted rhizomes. All occur in México and Guatemala.

Erigeron sect. **Karvinskia** Nesom, sect. nov. TYPE: **E. karvinskianus* DC.

> Plantae perennia, folia basalia decidua ab florescentia, folia caulinae obovatae dentatae plus minusve pariter distributae, gemmae erectae, corollae radii nec cincinnatae nec reflexae non clausae sursus nocte.

Additional species of sect. *Karvinskia*: **E. heteromorphus* B. Robinson, **E. irazuensis* Greenman and **E. pacayensis* Greenman.

Plants of this section are characterized by the following features: perennials from thin, woody taproots or short rhizomes, leaves mostly obovate, toothed, all cauline by flowering and distributed more or less equably on the stems, buds erect, ligules of the ray flowers neither coiling nor reflexing and not closing upwards at night. In addition to those listed above, there are two additional but undescribed species of sect. *Karvinskia* from México and Central America. The group is presently under study by me. Sect. *Karvinskia* may prove to be closely related to sect. *Linearifolii*, but the broader, toothed leaves and equal phyllaries of the former and the habit of the latter are distinctive.

Erigeron sect. **Linearifolii** (G. Don) Nesom, comb. nov. Based on *Aster* sect. *Linearifolii* G. Don in Loudon, Hort. Bot. 346. 1830. LECTOTYPE (Sundberg & Jones 1987): *A. graminifolius* Pursh (=*E. hyssopifolius* Michx.).

Erigeron sect. *Pycnophyllum* Cronq., Brittonia 6:141. 1947. TYPE: *E. foliosus* Nutt.

Sundberg & Jones (1987) lectotypified Don's sectional epithet to preserve an established one in *Aster*; by doing so, however, they moved Don's name into a position of priority over Cronquist's sect. *Pycnophyllum*.

Species of sect. *Linearifolii*: *E. aequifolius* H.M. Hall, *E. breweri* A. Gray, **E. chiangii* Nesom, *E. foliosus* Nutt., *E. hyssopifolius* Michx., *E. inornatus* A. Gray, **E. lepidopodus* (B. Robinson & Fern.) Nesom, *E. miser* A. Gray, *E. petrophilus* E. Greene, *E. rhizomatus* Cronq. and **E. scoparioides* Nesom.

In earlier publications, I did not clearly recognize the relationships of the three Mexican species of this section. *Erigeron lepidopodus* from Chihuahua and northern Durango, México, however, is clearly the sister species of *Erigeron rhizomatus*, endemic to Catron and McKinley counties, New Mexico. *Erigeron chiangii* and *E. scoparioides*, species of northeastern México, are probably sister taxa.

The species of sect. *Linearifolii* are characterized by the presence of numerous, linear or narrowly oblong, entire leaves, borne on short internodes and essentially uniform from base to near top of the plant. They are perennial, often with long, slender, caudex-like, lower branches. The buds are erect, the phyllaries are usually strongly graduated (though not in the type species) and the rays have ligules straight or slightly coiling at the tips.

Sect. *Olygotrichium* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:311. 1840. LECTOTYPE (designated here): *E. divaricatum* Nutt. (=*E. divergens* Torrey & A. Gray). Nuttall also included *E. tenuis* Torrey & Gray, *E. strigosus* Muhl. ex Willd. and *E. "occidentalis"* (?=*E. strigosus* Muhl. ex Willd.).

Heterochaeta DC., Prodr. 5:282. 1836; non Besser ex Schultes & Schultes, 1827. LECTOTYPE (designated here): *Erigeron pubescens* Kunth. De Candolle also included *E. gnaphalioides* Kunth (=*Conyza confusa* Cronq.) and four extra-American species.

Erigeron (sp.-group) *Philadelphici* Rydb., Fl. Colorado 359. 1906, in clave; non Small, 1933. TYPE: *E. philadelphicus* L.

Erigeron (sp.-group) *Bellidiastra* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. bellidiastrum* Nutt.

Erigeron (sp.-group) *Divergentes* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. divergens* Torrey & A. Gray.

Erigeron (sp.-group) *Flagellares* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. flagellaris* A. Gray

Species of sect. *Olygotrichium*: *E. bellidiastrum* Nutt., **E. bigelovii* A. Gray, **E. calcicola* Greenman, *E. colomexicanus* A. Nelson, *E. divergens* Torrey & A. Gray (incl. *E. solisaltator* Nesom), **E. dryophyllus* A. Gray, *E. flagellaris* A. Gray, **E. fundus* Nesom, *E. geiseri* Shinners, *E. gilensis*

Woot. & Standl., **E. gypsoverus* Nesom, *E. lemmonii* A. Gray, *E. lobatus* A. Nelson, **E. metrius* S.F. Blake, **E. mihianus* S.F. Blake, *E. mimegletes* Shinners, *E. modestus* A. Gray, *E. multiceps* E. Greene, **E. onofrensis* Nesom, *E. philadelphicus* L., **E. pinkavii* B. Turner, *E. proselyticus* Nesom, **E. pubescens* Kunth, *E. quercifolius* Lam., *E. religiosus* Cronq., *E. sionis* Cronq., *E. tenellus* DC., *E. tenuis* Torrey & A. Gray, **E. turnerorum* Nesom, **E. unguiphyllus* Nesom, **E. velutipes* Hook. & Arn. and **E. versicolor* (Greenman) Nesom.

Erigeron sect. *Olygotrichium* is a relatively large but well defined section. The species are primarily from the southwestern United States and México, with a small group from the eastern United States and the Antilles. They are mostly taprooted annuals or biennials, and though perennials are also included, no other section of *Erigeron* has so many species of plants of annual-biennial duration. They have prominently lobed or toothed leaves, nodding buds, small heads and narrow ligules often with a lilac midstripe on the lower surface. The ligules close upwards at night, neither reflexing nor coiling with maturity. This ligule behavior apparently is unique among the sections of *Erigeron*, but it is known from other genera of Astereae (e.g., *Aphanostephus* and at least some species of *Townsendia*). Four species, *E. mimegletes*, *E. versicolor*, *E. gilensis* and an undescribed species from Chihuahua, are epappose.

A group of inter-related species from the Antilles also appears to belong in sect. *Olygotrichium*: *E. caeruleus* Urban, *E. dissectus* Urban, *E. jamaicensis* L. and *E. pinetorum* Urban. *Erigeron psilocaulis* Urban differs from these in its non-clasping leaves but probably is part of the same lineage, as is the suffrutescent *E. darrellianus* Hemsley.

Relationships among the species of sect. *Olygotrichium* of the eastern and south-central United States are complex. *Erigeron philadelphicus, E. quercifolius* and *E. caeruleus* (and its relatives) appear to be closely related. *Erigeron tenuis, E. tenellus* , *E. geiseri* and *E. turnerorum* (northern México) form a closely knit group. *Erigeron tenuis*, in turn, is very similar to *E. strigosus* of sect. *Phalacroloma*. Further comments on the possible relationship between sect. *Olygotrichium* and sect. *Phalacroloma* are found under the latter.

As pointed out by Cronquist (1947), *Erigeron glabellus* (sect. *Fruticosus*) is in some ways (particularly its short-lived duration and numerous ray flowers with narrow ligules) similar to species of sect. *Olygotrichium*, and this species may indicate a possible direction of common ancestry for the two sections.

In Cronquist's view, sect. *Olygotrichium* comprised 20 species. One of these, *E. calvus* Coville, I consider to be a synonym of *E. divergens* and another, *E. plateauensis* Cronq., a synonym of *E. modestus.* Although Cronquist placed *E. multiceps* E. Greene in sect. *Erigeron* because of its perennial duration, it is, as he noted, most closely related to *E. divergens* and belongs in sect. *Olygotrichium*. Several species cited by Cronquist as members of sect. *Olygotrichium* are better placed in different groups: *E. myrionactis* Small (=*E. procumbens*, sect. *Cincinnactis*), *E. neomexicanus* A. Gray and *E. oreophilus* Greenman, both of which were included by Cronquist in *E. delphinifolius* (sect. *Polyactis*), *E. glabellus* (sect. *Fruticosus*), *E. vernus* (sect. *Fruticosus*) and *E. pulchellus* (sect. *Fruticosus*). Comments on the last three species are found under sect. *Fruticosus*.

Erigeron sect. Osteocaulis Nesom, sect. nov. TYPE: *E. linearis* (Hook.) Piper

> Bases caulium et foliorum plerumque albido-induratae osseae, gemmae erectae, folia lineares vel oblanceolatae, corollae radii luteae vel caeruleae nec cincinnatae nec reflexae non clausae sursus nocte in specie una abscentes differt.

Erigeron (sp.-group) *Lutei* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. luteus* A. Nelson [=*E. linearis* (Hook.) Piper].

Additional species in section *Osteocaulis*: *E. barbellatus* E. Greene (rays blue/white), *E. bloomeri* A. Gray (rayless), *E. chrysopsidis* A. Gray, *E. elegantulus* E. Greene (blue/pink rayed) and *E. piperianus* Cronq.

Sect. *Osteocaulis* is a well defined natural group whose essential composition was recognized by Cronquist in 1947. It is characterized by the following: perennials from caudices with several, short, erect branches; bases of stems and petioles usually whitish-indurated, bony-textured; buds erect; leaves entire, linear, varying to narrowly oblanceolate in *E. barbellatus*, stiffly erect; ligules of ray corollas not reflexing or coiling, yellow in three species, bluish in three, one species rayless. The only other yellow-rayed species of *Erigeron* in North America is *E. aureus*, which is a member of sect. *Erigeron*.

Several species of *Erigeron* sect. *Asteroidea* also have whitish petiole bases (e.g., *E. nanus, E. rydbergii*) but the margins are ciliate and the cellular texture is different from that in sect. *Osteocaulis*.

Cronquist (1947) did not make any comment regarding the putative relationships of *Erigeron filifolius*, but he did include it as a side branch among the species of sect. *Osteocaulis* in his "probable relationships" diagram. *Erigeron filifolius*, however, lacks both the yellow rays and strikingly indurated stem/petiole bases of the taxa that make section *Osteocaulis* unusual, and I have placed it in sect. *Asteroidea*.

Sect. *Phalacroloma* (Cass. in Cuvier) Torrey & A. Gray, Fl. N. Amer. 2(1):175. 1841. Based on *Phalacroloma* Cass. in Cuvier, Dict. Sci. Nat. 39:404. 1826. TYPE: *P. obtusifolia* Cass. (=*E. strigosus* Muhl.

ex Willd.). Cassini also included *P. acutifolia* Cass. [=*E. annuus* (L.) Pers.] in the genus.

Diplemium Rafin., Fl. Tellur. 2:50. 1836. LECTOTYPE (designated here): *Erigeron strigosus* Muhl. ex Willd. Rafinesque also included *Erigeron nervosus* Willd. [=*Heterotheca graminifolia* (Michx.) Elliott], *Erigeron quercifolius* Lam. and *Erigeron carolinianus* L.

Erigeron (sp.-group) *Ramosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. ramosus* (Walter) B.S.P. (=*E. strigosus*).

Erigeron (sp.-group) *Annui* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *E. annuus* (L.) Pers.

Cassini was not sure whether *Phalacroloma obtusifolia* might be the same species as *Erigeron hyssopifolius* Michx. or *E. carolinianus* L. "This confusion commenced with Pursh, who erroneously adduced the figure of Dillenius and the *E. Carolinianus* as synonyms of the *E. hyssopifolium* of Michaux" (Gray 1841). This putative synonymy was repeated by Cassini, de Candolle and Lessing. Cassini's description of the pappus and discussion of the characters of *Phalacroloma* leave little doubt, however, as Gray (1841) early realized, that the type was *E. strigosus* (see Fernald 1944, for further comments on the identity of *Erigeron carolinianus*).

Torrey & Gray (1841) included as members of sect. *Phalacroloma*: *E. strigosus, E. annuus, E. tenuis* and *E. divergens*, the last two of sect. *Olygotrichium.* Cronquist (1947) included only the two species lacking pappus bristles on the ray achenes, *Erigeron strigosus* and *E. annuus*, but, as he noted, *E. tenuis* is very similar to *E. strigosus* and sect. *Phalacroloma* may be only artificially separated from sect. *Olygotrichium.* Both species of sect. *Phalacroloma* are annuals with slightly to prominently nodding buds. The leaves of *E. annuus* are strongly toothed; those of *E. strigosus* vary from entire to toothed.

Chromosome counts of *Erigeron annuus* have all been triploid; diploid and various polyploid populations of *E. strigosus* have been reported. I speculate that *E. annuus* may be of hybrid origin between *E. strigosus* and some other species of the eastern United States, *E. philadelphicus* being the most conspicuous candidate.

Sect. *Polyactis* (Less.) Nesom, Phytologia 66:416. 1989. Based on *Polyactis* Less., Syn. gen. Comp. 188. 1832. TYPE: *Erigeron delphinifolius* Willd. *Polyactidium* DC., Prodr. 5:281. 1836.

Stenactis Cass. in Cuvier, Dict. Sci. Nat. 37:485. 1825. TYPE: *Erigeron delphinifolius* Willd. Non *Stenactis* sensu Nees, 1832; non sensu Less., 1832; non *E.* sect. *Stenactis* Torrey & A. Gray, 1841.

Achaetogeron A. Gray, Mem. Amer. Acad. Arts, n. ser. 4 (Pl. Fendl.):72.

1849. TYPE: *Achaetogeron wislizeni* A. Gray [=*Erigeron wislizeni* (A. Gray) E. Greene].

Species of sect. *Polyactis*: **E. annuactis* Nesom, **E. basaseachensis* Nesom, **E. caulinifolius* Nesom, **E. circulis* Nesom, **E. coroniglandifer* Nesom, **E. dactyloides* (Greenm.) Nesom, **E. delphinifolius* Willd., **E. eruptens* Nesom, **E. griseus* (Greenm.) Nesom, **E. inoptatus* A. Gray, **E. nacoriensis* Nesom, *E. neomexicanus* A. Gray, *E. oreophilus* Greenman, **E. podophyllus* Nesom, **E. polycephalus* (Larsen) Nesom, **E. rhizomactis* Nesom, **E. seemannii* (Schultz-Bip.) E. Greene, **E. subacaulis* (McVaugh) Nesom and **E. wislizeni* (A. Gray) E. Greene.

These species are characterized for the most part by pinnatifid or coarsely toothed leaves, arching-pendant buds, ligules that sharply reflex at the tube-ligule junction and a pappus of bristles that are basally caducous or completely lacking. All occur in western and south-central México; two of them, *E. oreophilus* and *E. neomexicanus*, also are found in the southwestern United States. See Nesom (1989a) for details and a discussion of typification of the generic synonyms noted here.

Erigeron sect. **Scopulincola** Nesom, sect. nov. TYPE: *E. scopulinus* Nesom & Roth

> Plantae parvulae rhizomatosae scopuli habitantes, folia oblanceolati-spathulata, corollae radii reflexae.

Additional species in sect. *Scopulincola: E. kachinensis* Welsh & Moore, *E. leiomerus* A. Gray and *E. pringlei* A. Gray.

These species from the southwestern United States appear to form a well defined natural group. The habitat of each is in cracks and crevices of rock faces and cliffs. All are rhizomatous perennials with entire, oblanceolate-spatulate leaves, erect buds and ray flowers with prominently reflexing ligules. In their leaves and habit, these plants are similar to those of sect. *Spathifolium*, but the peculiar habitat, distinctive rhizomes (vs caudex branches) and reflexing ligules set them apart.

Erigeron sect. **Spathifolium** Nesom, sect. nov. TYPE: *E. tener* (A. Gray) A. Gray

> Plantae parvae monocephalae ramis brevibus caudicis, indumentum strigillosum trichomatum alborum arcte adpressorum brevium rigidorum acutorum, folia oblanceolati-spathulatae, gemmae erectae, et corollae radii nec cincinnatae nec reflexae non clausae sursus nocte.

Additional species in sect. *Spathifolium: E. acomanus* Spellenberg & Knight ined, *E. cavernensis* Welsh & Atwood, *E. cronquistii* Maguire, *E. tener* (A. Gray) A. Gray, *E. tweedyi* Canby and *E. uncialis* S.F. Blake.

These six species comprise a relatively well defined natural group of mostly small perennials with long or short caudex branches, ultimately from a taproot, entire, oblanceolate-spatulate leaves, a strigillose indument of closely appressed, white, short, stiff and sharp-pointed hairs; erect buds and ligules that neither coil nor reflex. The stem pubescence of *E. uncialis* is longer and spreading but otherwise similar. The stems of these plants are simple and monocephalous, except for those of *E. tweedyi*, which usually are few branched.

Earlier, Nesom & Roth (1981) tentatively placed *Erigeron cronquistii* closer to sect. *Scopulincola.* Ake (1984), however, as well as Maguire (1944) in its original description, correctly recognized the relationship of *E. cronquistii* with *E. tener.* Atwood & Welsh (1988) noted in their discussion that *E. cavernensis* is "evidently allied to *E. simplex*," but they correctly contrasted it with *E. uncialis*, to which it is most similar, in the diagnosis.

The habit and peculiar pubescence of plants of sect. *Spathifolium* are similar to those in sect. *Wyomingia*, and there is a possibility of a close relationship between the two groups.

Erigeron sect. **Spinosi** (Alexander in Small) Nesom & Sundberg, comb. nov. Based on *Aster* (sp.-group) *Spinosi* Alexander in Small, Man. Southeastern Fl. 1365. 1933, in clave. *Aster* sect. *Spinosi* (Small) A.G. Jones, Brittonia 32:233. 1980. TYPE: *Aster spinosus* Benth. (=*Erigeron ortegae* S.F. Blake)

Additional species in sect. *Spinosi: E. oxyphyllus* E. Greene.

Sundberg (1986) concluded that *A. spinosus* is better placed in *Erigeron* than *Aster*, but he did not discover that it has such a close relative already placed in *Erigeron.* The similarity, however, between *E. oxyphyllus* and *A. spinosus* is striking. Plants of both produce stems that are 5-25 dm tall, strictly erect, green but somewhat ligneous, glabrous and striate. Further, both are perennial and usually produce many simple stems from a woody, rhizomatous base. The entire leaves are produced early in the season and are quickly deciduous, usually leaving only the green stems by flowering. In both species, the buds are erect, the phyllaries strongly graduated in 4-5 series and the heads solitary or in loose corymbs. On the other hand, the achenes of *E. oxyphyllus* are strigose and have 2-4 thick, orange, resin-filled ribs, while those of *A. spinosus* are glabrous, have 5, thinner, light-colored nerves and are not so strongly compressed. The phyllaries with three, orange-resinous veins emphasized by Sundberg as characteristic of *A. spinosus* are apparent on some plants of *E. oxyphyllus* (e.g., *Peebles & Harrison 5270* [LL]) but not on others. Plants of *E. oxyphyllus* are not spiny, but neither are some forms of *A. spinosus.*

Cronquist (1947) described *Erigeron oxyphyllus* as a "peculiar and well-marked species ... taxonomically somewhat isolated" but probably related to

E. arenarioides. Plants of the latter have erect buds and strongly graduated phyllaries, but in habit they are much smaller with thinner stems and have persistent basal and cauline leaves, and I have placed them in a different section.

The nomenclature and infraspecific taxonomy of *Aster spinosus* will be treated by Sundberg (in prep.).

The addition of a third species, which is from México and yet undescribed, will somewhat alter the circumscription of sect. *Spinosi.* This will be discussed in the formal proposal of the species (Sundberg & Nesom [in prep.]).

Besides *Aster spinosus*, Jones (1980) also included *A. intricatus* (A. Gray) Benth. (=*Leucosyris* E. Greene) in her *Aster* sect. *Spinosi.* See Nesom et al. (in press) for additional comments on the latter species, which is not part of the same group as *A. spinosus.*

Sect. *Tridactylia* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:310. 1841. TYPE: *E. compositus* Pursh. Monotypic as recognized by Nuttall.

Erigeron series *Multifidi* Rydb. ex Macbride & Payson, Contr. Gray Herb. 49:73. 1917. Based on *Erigeron* (sp.-group) *Multifidi* Rydb., Fl. Colorado 359. 1906, in clave. LECTOTYPE (designated here): *E. compositus* Pursh. *Erigeron* (sp.-group) *Compositi* Rydb., Fl. Rocky Mts. 896. 1918, in clave (Rydberg changed the name of this group in 1918). Macbride & Payson also included *E. pinnatisectus* (A. Gray) A. Nelson.

Additional species in sect. *Tridactylia: E. allocotus* S.F. Blake, *E. basalticus* Hoover, *E. flabellifolius* Rydb., *E. mancus* Rydb., *E. pallens* Cronq., *E. pinnatisectus* (A. Gray) A. Nelson, *E. purpuratus* E. Greene, *E. salishii* Douglas & Packer, *E. trifidus* Hook. and *E. vagus* Payson. Becker (1976) described *E. mexiae* Becker, which sometimes has apically tridentate leaves, as a "connecting link" between sect. *Erigeron* and sect. *Tridactylia* and it may be a member of the latter.

Most of the species of sect. *Tridactylia* have pinnatifid leaves; in several, the leaves are apically trilobed. In all species the leaves are non clasping, the buds are erect and the ligules neither coil nor reflex. Also, they are perennials with a strong tendency to produce rhizome like caudex branches.

Sect. *Wyomingia* (A. Nelson) Cronq., Brittonia 6:140. 1947. Based on *Wyomingia* A. Nelson, Bull. Torrey Bot. Club 26:249. 1899. TYPE: *E. pulcherrimus* Heller [=*Wyomingia pulcherrima* (Heller) A. Nelson].

Erigeron (sp.-group) *Cani* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. canus* A. Gray

Erigeron (sp.-group) *Tetrapleuri* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *E. tetrapleuris* (A. Gray) Heller (=*E. utahensis* A. Gray).

The species of sect. *Wyomingia* are taprooted perennials, and they have entire, more or less linear leaves, a strigillose vestiture of very short and closely appressed hairs, erect buds and prominently coiling ligules. I recognize two groups within the section and list the species accordingly.

1. The *E. pulcherrimus* group: *E. argentatus* A. Gray, *E. canus* A. Gray, *E. parishii* A. Gray, *E. pulcherrimus* and *E. utahensis* A. Gray.

These species have multi-nerved [(2-)4-10(-14)] achenes, a feature restricted mostly to this group. The achenes of *Erigeron* sect. *Spinosi*, however, also may have 4 to 5 ribs, as may those of *E. peregrinus* (sect. *Fruticosus*) and *E. lepidopodus* and *E. rhizomatus* (sect. *Linearifolii*).

2. The *E. compactus* group: *E. carringtonae* Welsh, *E. compactus* S.F. Blake, *E. consimilis* Cronq., *E. nematophyllus* Rydb. and *E. untermannii* Welsh & Goodrich.

Erigeron compactus, *E. consimilis* and *E. nematophyllus* were noted by Cronquist (1947) to be "apparently not far removed from the line of descent of the section *Wyomingia*." They lack the multinerved achenes characteristic of the *E. pulcherrimus* group and tend to be smaller in stature but are otherwise very similar. Some plants of *E. pulcherrimus*, however, are small and nearly identical in habit to those of *E. compactus*. *Erigeron nematophyllus* is obviously more similar to *E. utahensis* in its habit of relatively tall, branching stems, which suggests that the taxonomic use of achenial nerves may result in an artificial division, at least in this section. Welsh (1983) hypothesized that *E. untermannii* and *E. carringtonae* are most closely related to *E. compactus*, and they are included here on that basis.

Erigeron rhizomatus, which was included by Cronquist (1947) in sect. *Wyomingia*, is placed in sect. *Linearifolii* in the present treatment with its sister species, *E. lepidopodus*.

SOUTH AMERICAN GROUPS – POSITION IN *ERIGERON* UNKNOWN

Erigeron sect. *Leptostelma* (D. Don) Benth. & Hook., Gen. Pl. 2:280. 1873. Based on *Leptostelma* D. Don in Sweet. TYPE: *Leptostelma maximum* D. Don [*E. maximus* (D. Don) DC.].

Additional species of sect. *Leptostelma* (see Solbrig 1962): *E. tucumanensis* Cabrera and *E. tweediei* Hook. & Arn.

Darwiniothamnus Harling, Acta Horti Berg. 20(3):108. 1962. TYPE: *D. tenuifolius* (Hook. f.) Harling (=*Erigeron tenuifolius* Hook. f.).

The two species of *Erigeron* that occur on the Galapagos Islands (*E.tenuifolius* and *E. lancifolius* Hook. f.) were segregated as the genus *Darwiniothamnus* by Harling (1962). These plants were said to differ from *Erigeron* in the following features: habit completely fruticose; involucre obconic to narrowly campanulate; phyllaries strongly imbricate in 4-6 unequal series, the outer grading into peduncular bracts; ray flowers more numerous than the disc flowers; achenes "slightly but distinctly" dimorphic, the ray achenes longer with fewer and weaker nerves than the disc achenes; and the embryo sac development monosporic.

The putatively distinctive features in *Darwiniothamnus* of phyllary arrangement and involucral shape can be found in many species in different sections of *Erigeron*. Examples of slight achenial dimorphism can be found in sect. *Fruticosus*, sect. *Polyactis* and probably others, although the usual case is for the ray achenes to have more numerous and thicker ribs than those of the disc. The reduced number of disc flowers in the Galapagos plants is unusual in continental American species of *Erigeron*, but a number of Caribbean species have very small heads and a correspondingly reduced number of flowers. The embryology of relatively very few species (ca 25, none from South America) of *Erigeron* has been investigated (Harling 1951). Two of these, however, were shown by Harling himself to have strictly monosporic embryo sac development [*E. philadelphicus* (sect. *Olygotrichium*) and *E. peregrinus* (sect. *Fruticosus*]; other species are variably mono-, bi- or tetra-sporic. In summary, the primary difference separating the two Galapagos Islands species from others of the genus is the peculiar, shrubby habit, and in my estimation this is inadequate justification for segregating them as a different genus. A case might be made, however, for regarding them as a section, but I leave this to someone more familiar with South American taxa.

The tendency for the evolutionary development of a woody habit in insular plants is well documented. Carlquist (1974) provided examples of Compositae and many other families in which genera with herbaceous mainland species have developed woody, insular species. Among those in the Compositae are insular species of *Bidens, Centaurea, Dubautia, Perityle, Remya, Robinsonia, Senecio, Sonchus* and *Stephanodoria*. As in *Darwiniothamnus*, most of these are rosette trees or rosette shrubs with long, mostly unbranched stems and leaves clustered near the stem tips.

Besides those of the Galapagos Islands, suffrutescent species of *Erigeron* with similar habits also have developed on the Revillagigedo Islands (noted below), the Bahama Islands (*E. darrellianus* Hemsl., tentatively placed in sect. *Olygotrichium*) and the Juan Fernandez Islands (see comments following *Terranea*). Among these, the species of the Revillagigedo Islands are most similar in habit and other characters to those of the Galapagos Islands, and in contrast to I.M. Johnston's original hypothesis of the relationship of the latter with sect. *Caenotus*, I place them in *Erigeron* sect. *Cincinnactis*, which otherwise comprises species of the Mexican mainland. The habital similarity in these insular taxa almost certainly has resulted from convergent evolution.

Terranea Colla, Mem. Reale Accad. Sci. Torin. 38:11. 1835. TYPE: *T. fernandezia* Colla [=*E. fernandezia* (Colla) Harling; non *E. fernandezianus* Solbrig].

Erigeron fernandezia was included by Solbrig (1962) in his broad concept of sect. *Erigeron*. Three other closely related species of *Erigeron* occur in the Juan Fernandez Islands and probably evolved from a single common ancestor from the mainland, perhaps *E. leptorhizon* DC. (Valdebenito et al. 1985).

Astradelphus Remy, Ann. Sci. Nat. Bot. ser. 3. 12:185. 1849. (=*Gusmania* Remy in C. Gay, Fl. Chile 4:12. 1849; non *Guzmania* Ruiz & Pavon, 1802). TYPE: *A. chilensis* (Remy) Remy (=*Gusmania chilensis* Remy; =*Erigeron remyanus* Wedd., Chlor. And. 1:195. 1857).

According to Solbrig, *Erigeron remyanus* is perhaps a member of sect. *Erigeron* (sensu Solbrig 1962).

GROUPS TRANSFERRED FROM *ERIGERON* TO OTHER GENERA

1. *CONYZA*

Erigeron sect. *Caenotus* Nutt., Gen. Plant. 2:148. 1818. TYPE: *E. canadensis* L. [=*Conyza canadensis* (L.) Cronq.]. *Caenotus* (Nutt.) Rafin., Fl. Tell. 2:50. 1836. *Conyza* sect. *Caenotus* (Nutt.) Cronq. ex Cuatr., Webbia 24:211. 1969.

Erigeron sect. *Multiflori* G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (designated here): *E. canadensis* L. [=*Conyza canadensis* (L.) Cronq.]. Don also included 22 other species of a number of disparate lineages.

I regard sect. *Caenotus* as a synonym of sect. *Conyza*, which includes *C. canadensis* (L.) Cronq., *C. bonariensis* (L.) Cronq., *C. ramosissima* Cronq., *C. primulaefolia* (Lam.) Lourteig & Cuatr. [=*C. chilensis* Spreng.] and others. See Nesom (in press) for further comments and synonymy.

2. *CELMISIA*

Pappochroma Rafin., Fl. Tellur. 2:48. 1836. TYPE: *P. uniflora* Rafin. (=*Erigeron pappochroma* Labill., an Australian species, perhaps *Celmisia* Cass., 1825).

3. *ORITROPHIUM*

Erigeron sect. *Oritrophium* (Kunth) Benth. & Hook., Gen. Pl. 2:280. 1873. Based on *Aster* sect. *Oritrophium* Kunth. LECTOTYPE (Cuatrecasas 1961): *Aster pellitus* Kunth [=*Oritrophium peruvianum* (Lam.)

Cuatr.]. *Celmisia* sect. *Oritrophium* (Kunth) Solbrig. *Oritrophium* (Kunth) Cuatr.

4. *TRIMORPHA*

Erigeron sect. *Trimorpha* (Cass. in F. Cuvier) DC., Prodr. 5:290. 1836. *Trimorpha* Cass., Bull. Sci. Soc. Philom. Paris 1817:137. 1817. TYPE: *Trimorpha vulgaris* Cass. in Cuvier, Dict. Sci. Nat. 55:324. 1828 (=*E. acris* L.). *Trimorphaea* Cass. in Cuvier, Dict. Sci. Nat. 37:462. 1825. *Erigeron* subg. *Trimorpha* (Cass.) M. Pop.

Erigeron (sp.-group) *Acres* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *E. acris* L.

I regard *Trimorpha* as a distinct genus more similar to *Conyza* than *Erigeron* (Nesom 1989b).

5. GENUS UNKNOWN

Erigeron sect. *Submultiflori* G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (designated here): *E. carolinianus* L. Don also included *Erigeron villarsii* Bell. (=*Erigeron atticus* Villars of sect. *Trimorpha* in his sect. *Submultiflori*.

Fernald (1944) discussed the identity of *Erigeron carolinianus* L. but could only conclude that he could not identify it "unless it was something not originally from Carolina or, as Dillenius thought, an abnormal individual." It is certainly not an *Erigeron*, and I agree with Fernald that it is unlike any species of *Euthamia*. It is more *Solidago*-like, but it is likely that the identity of this Linnaean epithet will remain equivocal. Because Don's sect. *Submultiflori* was essentially meaningless in comprising two extremely divergent species from different genera, I feel justified in attaching it to a species name that itself has little chance of being clearly identified. To choose *E. villarsii* as the lectotype would necessitate replacing the widely used and well established name of sect. *Trimorpha*.

Tanaxion Rafin., Fl. Tellur. 2:51. 1836. TYPE: *T. tomentosum* Rafin. (=*Erigeron bahamensis* Scop.). I do not know the identity of this plant.

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